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Further Evidence for Monocular Determinants of Perceived Plaid Direction

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This report adds to existing evidence that a monocular, feature-sensitive motion mechanism is involved in two-dimensional (2-D) motion processing, and also accounts for an earlier, unexplained result [Alais *et al.*(1994) *Vision Research, 34*, 1823–1834]. The central finding is that the perceived direction of a monocularly viewed type II plaid changes over a period of continuous exposure such that post-adaptation direction judgements exhibit more of the component-direction bias known to occur with these stimuli than pre-adaptation judgements. These adaptation effects are confined to the adapted eye: when the adapting stimulus is presented to one eye, pre- and post-adaptation direction judgements made with the other, non-adapted eye are identical. These results strongly suggest the involvement of a monocular motion mechanism in two-dimensional motion processing, in addition to the more commonly presumed binocular mechanisms.

Motion perception Motion aftereffect Adaptation Direction perception

INTRODUCTION

In recent years, a great deal of research has focused on how the visual system processes the motion of two-dimensional (2-D) objects. One laboratory technique frequently used to investigate this question involves the use of plaid stimuli. Plaids are 2-D stimuli which are designed to mimic the motion of real objects in the visual environment and are composed of superimposed, independently moving gratings. These stimuli can be seen to move coherently in a single direction under conditions where the component gratings are the same or similar in terms of contrast and spatial frequency (Adelson & Movshon, 1982). The Intersection of Constraints (IOC) model has been offered to account for the perceived direction of coherently moving plaids (Movshon *et al.*, 1985) and postulates the involvement of the middle temporal (MT) visual area as the site of the crucial mechanism integrating the independent component motions signalled in visual area one (V1). However, there are now a number of recent studies indicating the involvement of a monocular mechanism in both the coherence and direction perception of 2-D motion (Alais *et al.*, 1994; Burke *et al.*, 1994; Burke & Wenderoth, 1993b; Wenderoth *et al.*, 1995). This does not fit easily with the IOC model and suggests that the latter is incomplete because MT is a highly binocular area (Felleman & Kaas, 1984).

The first of these studies showed that there were duration differences between plaid motion aftereffects (MAEs) induced by simultaneous and successive adaptation to the two plaid components (Burke & Wenderoth, 1993b; Wenderoth *et al.*, 1995). We argued that (i) the important difference between successive and simultaneous adaptation is the presence of the grating intersections (the dark and light features visible on a plaid known as "blobs") in the simultaneous case, and their absence in the successive case; and (ii) there is a mechanism which responds directly to the motion of the blobs. By this explanation, it is the additional adaptation of this feature-sensitive motion mechanism (FSMM), in the simultaneous case, which accounts for the MAE duration differences. However, it was also shown that if adaptation and testing are of different eyes, the MAE duration differences are eliminated, such that the simultaneously adapted MAE is reduced to the duration of the successively adapted MAE. We concluded, therefore, that the feature-sensitive mechanism responsive to the motion of the blobs is monocular and so did not contribute to the interocularly measured MAE. This interocular transfer (IOT) procedure has also revealed monocular determinants of the perceived *direction* of 2-D MAEs (Alais *et al.*, 1994) and the perceived coherence of moving 2-D patterns (Burke *et al.*, 1994).

While the IOT procedure has so far provided good evidence for a role for a monocular mechanism in determining the perceived direction of 2-D MAEs, there is, as yet, no direct evidence that a monocular mechanism influences perceived plaid direction *while the plaid is in*

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motion. Ordinarily, in line with the traditional ratio (Barlow & Hill, 1963) or distribution shift (Mather, 1980) model of the MAE, we would simply assume that effects evident in the testing of the MAE reflect the state of the motion mechanisms fatigued during the adaptation period, yet, we have also obtained evidence of a dissociation between perceived plaid direction during adaptation and the perceived direction of the resulting MAE (Alais *et al.*, 1994). Thus, assuming such a simple correspondence between the direction of adaptation and the resulting MAE direction might not be valid, and it was a consideration of these results which prompted the present study.

EXPERIMENT 1

Ferrera and Wilson (1987) classified drifting plaids into two distinct types. Type I plaids are those in which the component gratings drift in directions on either side of the IOC resultant, and type II plaids are those in which the components both drift in directions on the same side of the IOC resultant. There are a number of differences in the way in which these types of plaids are perceived, but the most relevant for this study is the fact that type II plaids appear to drift in a direction which is significantly biased towards the component directions, and away from the IOC-predicted direction. Burke and Wenderoth (1993a) proposed that this misperception could be a consequence of interactions between the cells signalling the component motions because, as the components of a type II plaid must drift in similar directions, they generate overlapping distributions of activity in 1-D motion-sensitive neurons. As a consequence of lateral inhibition between these populations of neurons, the activity peaks in these distributions are shifted apart, with result that the component motion directions become signalled as being further apart than the actual motions of the components. Burke and Wenderoth suggested that these altered signals then feed forward into the neural mechanism which computes 2-D motion from 1-D component signals, where, according to the IOC rule, it would always produce a component-biased plaid direction and thus account for type II plaid misperception.

By manipulating the contrast, spatial frequency and drift rate of type II plaid components, Alais *et al.* (1994) further classified optimal blob plaids and non-optimal blob plaids. Optimal blob plaids (high contrast, high spatial frequency, low drift rate) were defined as those type II plaids which produced the biggest direction differences between simultaneously and successively adapted MAEs, since MAEs generated by the latter method contain no signal due to the adapted FSMM. Non-optimal blob plaids were essentially the opposite of optimal blob plaids (low contrast, low spatial frequency, high drift rate) and produced no direction differences between simultaneously and successively adapted MAEs. The lack of any difference between the adaptation methods suggests that non-optimal blob plaids are effectively blobless and do not effectively activate the FSMM in the simultaneous case.

We reconciled the evidence implicating a monocular FSMM with the earlier evidence suggesting the existence of an IOC mechanism, presumably binocular (Movshon *et al.*, 1985; Felleman & Kaas, 1984), by proposing that there are two independent mechanisms activated by 2-D motion [although we have evidence indicating that one may inhibit the other—Burke *et al.* (1994)]. In the case of type II plaids, the two mechanisms will be signalling different directions of motion because the output of the IOC mechanism will be affected by the miscoded component motions mentioned above, but the FSMM will not, since the blob features of the plaid always move in the actual plaid direction, regardless of whether the plaid is of type I or type II. This means that the perceived direction of type II plaids should be substantially influenced by whether they contain optimal or non-optimal blobs. Type II plaids containing non-optimal blobs would only activate the FSMM weakly or not at all, and should thus be substantially misperceived since they would rely on the miscoded component directions and the erroneous IOC resultant. Optimal blob plaids should activate the FSMM more strongly and thus give greater weight to the motion of the blobs in the percept of plaid direction, resulting in more veridical direction perception. In the event, these were precisely the results we obtained (Alais *et al.*, 1994).

Consistent with previous evidence that the FSMM is monocular, we also showed that the percieved direction of drift of optimal blob, type II plaids is affected by whether they are observed monocularly or binocularly. The rationale behind this manipulation was the assumption that binocular viewing would favour binocular mechanisms, since binocularly sensitive neurons, such as those in area MT where it is assumed that the IOC algorithm is implemented, require binocular stimulation to be maximally activated (Felleman & Kaas, 1984; Hubel & Wiesel, 1977). By this reasoning, we predicted that optimal blob plaids should appear to drift in a more veridical direction under monocular viewing than under binocular viewing. This follows because the synergistic activation of the IOC mechanism due to binocular viewing would be very much greater than its activation due to monocular viewing, which would effectively reduce the relative weight of the direction signalled by the monocular FSMM. On the other hand, the relative weight of the FSMM signal is negligible when non-optimal blob plaids are used, and so the direction signalled by the IOC mechanism remains predominant, irrespective of monocular or binocular viewing. For both stimuli, these were exactly the results we obtained (Alais *et al.*, 1994), which is consistent with the involvement of a monocular FSMM in determining perceived plaid direction. Experiment 1 of this report is a further test of this proposal using the IOT procedure.

Another reason for this experiment is our informal observations that the perceived direction of type II, optimal blob plaids change over a period of adaptation, whereas non-optimal blob plaids do not. It has already been reported that, for very short durations, type II plaid

direction becomes more veridical with increasing exposure time (Yo & Wilson, 1992). They reported that, initially, plaids are judged to move in the component vector sum direction and only approach the IOC direction after about 150 msec. Our observations concerned far longer durations of up to 30 sec. We noted that while the perceived direction of type II, optimal blob plaids were close to the IOC-predicted direction in the first few seconds, they became progressively *less* veridical over the exposure period. One explanation of this observation could be that the optimized blobs of this plaid vigorously activate the FSMM, such that its output is the dominant signal affecting perceived plaid direction, thus accounting for the near-veridical direction. However, as a consequence of its vigorous activation, the FSMM might also become quickly fatigued, which would give progressively more weight over time to the miscoded component directions and the IOC mechanism which integrates them. If support for such an explanation could be found, it would provide a potential explanation of the dissociated adaptation and MAE directions which Alais *et al.* (1994) reported. Moreover, if the FSMM is indeed monocular, then a 30 sec exposure period to a drifting plaid in one eye should have no effect on perceived plaid direction when measured with the other eye (the IOT procedure). Conversely, 30 sec of exposure to a drifting type II plaid in one eye should substantially alter the perceived plaid direction when it is subsequently judged with the same eye (the MON–MON procedure). Experiment 1 is a test this prediction.

Methods

Stimuli and aparatus. All stimulus displays were presented on the flat screen of a Tektronix 608 display monitor (P31 phosphor), interfaced with an Innisfree ("Picasso") image generator and a PDP 11/73 minicomputer. Plaid patterns were generated by temporally interleaving the two frames bearing the drifting components at 188 Hz. The Michelson contrast of each of the adapting plaid components, defined as $(L_{max} - L_{min}) / (L_{max} + L_{min})$, was 0.2, making the contrast of the adapting plaid 0.4. All patterns were displayed in a computer-generated aperture 6.5 deg in diameter (at the viewing distance of 57 cm), seen through a circular black mask, 6.75 deg in diameter.

A single type II plaid was used in this experiment. The true plaid direction was 90 deg (straight down), and the plaid components drifted towards 45 and 60 deg (to the right of straight down) at a rate of 2.8 and 3.4 Hz, respectively, and had a spatial frequency of 3 c/deg. These values make the plaid similar to the optimal blob plaids mentioned above. Since it was demonstrated in an earlier paper (Alais *et al.*, 1994) that non-optimal blob plaids do not exhibit any dissociation between direction judgements during adaptation and those of the resulting MAE, only the optimal blob plaid will be tested in this experiment. Liquid crystal shutters, mounted in front of the subject's eyes, and under the control of the experimenter, were used to effect the changes in viewing condition (from left eye to right eye, etc.). Subjects' heads were held in place with a padded chinrest and head clamp.

Procedure. Subjects sat in a darkened laboratory where the only light source was the display screen. Their task was to judge the perceived plaid direction both before and after a period of adaptation. They did this by rotating a computer generated pointer around the perimeter of the plaid pattern, using a control box in front of them. The two outside buttons caused the pointer to rotate and the subjects pressed the middle button when they were satisfied with the setting they had made. On each adjustment trial the pointer appeared at one of five randomly selected starting positions; 0, ±15 or ±30 deg with respect to the true direction of plaid drift. Subjects found the task relatively easy, but were given 15 practice trials so that they could make their judgements quickly. They were instructed to stare at the fixation point in the centre of the display for the entire time the pattern was present, and to make their settings as quickly as they could accurately be made.

Following the practice trials, subjects were exposed to the series of pre-adaptation/adaptation/post-adaptation sequences, in which the drifting plaid was continuously present. On each trial, the type II plaid would appear with the adjustable pointer and subjects quickly indicated the plaid direction. When the computer recorded their setting the pointer disappeared, initiating the 30 sec adaptation period. Following an auditory prompt 30 sec later, the pointer reappeared and the subjects were again required to indicate the perceived direction of drift. The second (post-adaptation) setting was recorded by the computer and a 60 sec rest period initiated, after which the sequence was repeated.

All viewing was monocular and subjects always used their dominant eye to make the pre-adaptation and post-adaptation settings. On MON–MON trials, the dominant eye was used throughout the pre-adaptation/adaptation/post-adaptation sequence, but on IOT trials the 30 sec of adaptation was of the other (non-dominant) eye. That is, on IOT trials, when subjects pushed the middle button to indicate the pre-adaptation direction, the pointer disappeared and the polarization of the liquid crystal shutters in front of their eyes reversed. Thus, during the adaptation period they viewed the pattern with their other eye. After the 30 sec of adaptation, the shutters reversed again, so that the post-adaptation setting was made using the same eye used to make the pre-adaptation setting.

The experiment was a simple 2 × 2 factorial design. The factors were test condition (pre-adaptation vs post-adaptation) and adaptation mode (IOT vs MON–MON). Each subject made four pre-adaptation and four post-adaptation settings under each of the MON–MON and IOT viewing conditions (a total of 16 direction judgements and eight adaptations).

Subjects. The 13 subjects were first year students at the University of Sydney, Australia, all had emmetropic or suitably corrected vision, and all were naive as to the aims of the experiment.

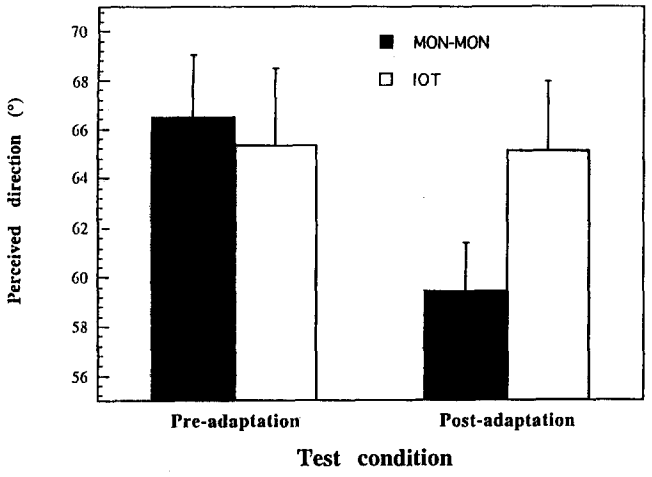

FIGURE 1. Judgements of perceived plaid direction as a function of test condition and adaptation mode. Pre-adaptation direction judgements are very similar in both MON–MON and IOT conditions, but differ significantly following a period of adaptation. This difference is mainly attributable to the MON–MON condition, where the motion adaptation and the pre- and post-adaptation direction judgements were made with the same eye. In this condition, the component-direction bias is greater following adaptation to the plaid (i.e., the plaid is seen less veridically, with respect to the IOC-predicted direction). In the IOT case, where direction judgements were made with the unadapted eye, pre- and post-adaptation direction judgements are identical. Note that error bars in Figs 1 and 2 are +1 SE, and that the actual plaid direction was directly downwards at 90 deg.

Results

As can clearly be seen from Fig. 1, the perceived direction of plaid drift only changed when the adapting plaid was presented to the same eye as was used to make the judgements (the MON–MON condition). The pre-adaptation and post-adaptation perceived directions are the same in the IOT condition, indicating that presenting the adapting pattern to the other eye made no difference to the perceived direction.

The average setting for each subject in each cell of the experiment was entered into a factorial analysis of variance (ANOVA). The ANOVA revealed a significant main effect of test condition ($F_{1,12} = 14.91$, $P < 0.005$) and a significant interaction between test condition and adaptation mode ($F_{1,12} = 10.32$, $P < 0.01$). The main effect of adaptation mode was not significant ($F_{1,12} = 0.65$, $P > 0.4$).

Discussion

The results of this experiment are consistent with the idea that a monocular mechanism makes a significant contribution to the perceived direction of type II plaids, and that prolonged exposure to such stimuli can fatigue it. These results are also consistent with the idea that a monocular FSMM is responding directly to the motion of object features (the blobs in the case of plaid stimuli) and can be added to the other reports reviewed in the introduction which implicate monocular determinants in 2-D motion perception. Such a mechanism has now been implicated as a determinant of the perceived direction of type II plaids, as well as in the perception plaid coherence (Burke *et al.*, 1994) and the perceived duration and direction of MAEs induced by drifting plaids (Alais *et al.*, 1994; Burke & Wenderoth, 1993a). There are, as yet, no data implicating such a mechanism in the perceived velocity of 2-D motion, although we plan to conduct future experiments to address this matter.

These data also suggest an explanation for the curious finding of Alais *et al.* (1994) that "...plaids with more- and less-optimal blobs appear to drift in directions 20 deg apart yet their aftereffects differ in direction by only 3–5 deg". This finding seemed curious because it is typically reported that MAEs are directionally opposite the *perceived* rather than the *actual* inducing motion, such as occurs with the barber pole illusion (Power & Moulden, 1992). However, in the Alais *et al.* study, this only occurred for the non-optimal blob plaids: the perceived direction of the optimal blob plaids were dissociated from their MAE directions by about 20 deg, with the MAE direction reflecting more of the component direction bias than the corresponding direction judgements. The discovery that the perceived direction of a type II plaid *changes* over a 30 sec adaptation period provides a potential explanation of this phenomenon. Since we have just established that the direction of optimal blob plaids changes over a period of adaptation, reflecting progressively more of the component direction bias, and since Alais *et al.* measured plaid directions at the beginning of the adaptation period, their measures of the adapting direction of the plaid are not likely to be entirely representative of the state of adaptation among direction-selective neurons. This is important because it is the neural imbalance in firing rates caused by the adapted motion directions that will determine the direction of the aftereffect. Thus, a more representative measure of the adapted directions might show that there is no dissociation of adapting and MAE directions at all. If this were so, it would provide a solution to the puzzling dissociation reported by Alais *et al.* which had seemed inexplicable in terms of conventional models of the MAE.

EXPERIMENT 2

Experiment 2 tests the potential explanation of the dissociation effect outlined in the discussion immediately above. It will do so by measuring perceived plaid direction at the beginning and end of a 30 sec adaptation period (as in expt 1), and comparing these directions with the perceived direction of the resulting MAE. It was not feasible to have the subjects make all three direction judgements on each trial. Instead, there were two types of trial. In the first type, subjects judged perceived plaid direction at the beginning of the adaptation period, and then again 30 sec later (as in expt 1). In the second type, subjects again indicated perceived plaid direction at the beginning of the adaptation period, but when the plaid stopped 30 sec later, they set the pointer to indicate the perceived direction of the MAE.

If the dissociation of perceived plaid directions during adaptation and during MAE testing is to be explained by

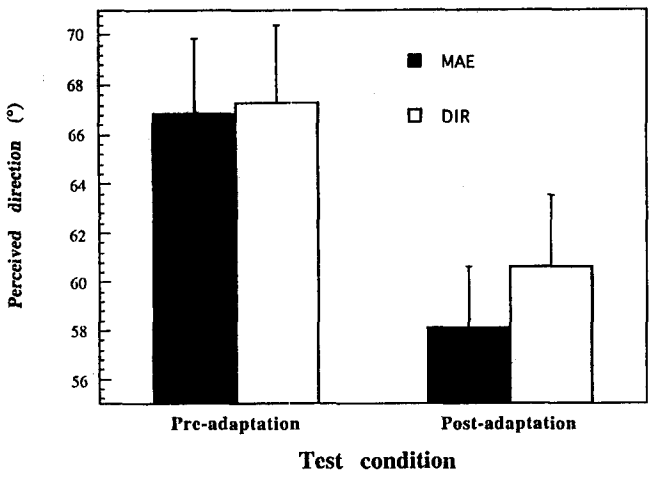

FIGURE 2. The column pairs in this graph show the data from two dependent variables, MAE direction (solid columns) and transformed direction judgements (open columns). The judged directions have had 180 deg subtracted so that they can be easily compared with the MAE data. Thus, in the post-adaptation test condition, where the values of MAE and direction are not statistically different, the data indicate that perceived plaid direction during adaptation and perceived MAE direction are effectively directly opposed. In the pre-adaptation test condition, the similar values of MAE and direction result from the fact that these are identical plaids being judged under identical conditions (see text). The crucial aspect of these data is that perceived MAE direction remains opposed to the perceived direction of the adapting plaid even when prolonged exposure to the stimulus causes a change in perceived plaid direction (see Fig. 1).

the results of expt 1, then the perceived plaid direction after 30 sec of adaptation should be close to directly opposite the perceived direction of the resulting MAE.

Methods

The methods were, for the most part, identical to those in expt 1. Ten new, naive subjects were used, and all viewing was with the dominant eye throughout. For the purposes of the analysis, this experiment is a 2 × 2 factorial design. Again, one factor was test condition (pre-adaptation vs post-adaptation), and the other was judgement type (perceived plaid direction vs MAE direction). Each subject made four judgements under each of the four conditions. For each subject, in each condition, the average of these four settings was entered into a 2 × 2 factorial ANOVA.

Results

As can be seen from Fig. 2, the predicted pattern of results was obtained. The important result is that the perceived MAE direction is not significantly different from the perceived direction (*minus* 180 deg) of the plaid in the post-adaptation phase ($t_9 = 0.92$, $P = 0.30$). The fact that perceived plaid direction in the pre-adaptation phase is the same under the MAE and direction conditions is expected, since these are identical plaids being judged under identical conditions.

Consistent with this graphical interpretation of the data, the ANOVA revealed a significant main effect of test condition ($F_{1,9} = 42.11$, $P = 0.0001$), but the main effect of judgement type ($F_{1,9} = 1.19$, $P = 0.30$) and the interaction ($F_{1,9} = 1.39$, $P = 0.27$) were not significant.

Discussion

Experiment 2 confirms the result reported by Alais *et al.* that the perceived direction of type II plaid MAEs is *not* opposite the direction in which the adapting plaid initially appears to drift. However, the crucial result of this experiment is that these MAEs *are* opposite the direction in which the plaid appears to drift at the end of the 30 sec adaptation period.

While the change in perceived type II plaid direction over time might seem unusual, it is not implausible with multi-component stimuli and it does support the explanation offered above that the original dissociation reported by Alais *et al.* can be explained by the plaid changing direction during adaptation and becoming less veridical. Moreover, the results from expt 1 provide strong evidence that the mechanism which is responsible for this change in perceived direction over time is monocular. This adds to evidence from a number of other findings which implicate the involvement of a monocular motion mechanism responsive to the motion of object features in 2-D motion processing.

GENERAL DISCUSSION

It is interesting to consider the findings reported here in terms of the 2-D motion perception model offered by Wilson *et al.* (1992) and extended by Wilson and Kim (1994). According to this model, following orientation filtering of a stimulus such as a plaid, two parallel motion pathways are involved in coding 2-D motion perception. In one, the Fourier pathway, the motion of the plaid's grating components is detected by motion energy units in area V1 (Adelson & Bergen, 1985; Van-Santen & Sperling, 1984), which then feed to units in area MT which in turn produce a cosine-weighted sum of the component motions. In the other, non-Fourier pathway, a process of full-wave rectification followed by additional orientation filtering at a lower spatial frequency is postulated to take place in area V2, so that motion energy units can be employed to detect non-Fourier motion and the motion of texture boundaries. These motion energy units are postulated to reside either in area V2 or in area MT using V2 output. The final stage of the model is the cosine-weighted combination of the output of the Fourier and non-Fourier pathways, followed by competitive feedback inhibition, to yield the direction of the 2-D pattern. Thus, while the Wilson model includes the detection of the grating component direction within the Fourier pathway, the non-Fourier pathway signals additional directional information which must be combined with the Fourier output to accurately represent 2-D motion perception.

Similarly, we have argued previously that output from a FSMM must be added to component-based calculations of pattern direction to accurately represent 2-D motion perception (Alais *et al.*, 1994; Burke *et al.*, 1994; Wenderoth *et al.*, 1995). The key difference between

our proposal and the Wilson model is that we consider the additional information for accurate 2-D motion perception to come from simple luminance-defined features, the so-called blobs in the case of plaid stimuli, whereas for Wilson the additional information comes from texture boundaries. With plaid stimuli, the blobs are simply local luminance peaks and troughs which are relevant because they are analogous to the texture or features which are normally visible on the surface of objects in our visual environment. Blobs are also important because they are particularly salient cues to object direction. This follows from the fact that they belong to the object itself and hence must have the same direction and velocity as the object. The texture boundaries to which Wilson's models refer are the borders between the beat patterns, which are clearly visible in a type II plaid, and the rows of elongated blobs which are oriented perpendicularly on either side of the beats. Thus, the texture boundary is jointly defined by the blobs and the beats. Texture boundaries are also evident, for example, in gratings defined by differences in the size of the texture elements.

Given that both blobs and beats define texture boundaries, and since manipulations of the blobs would necessarily also alter the beats (and thus the texture boundary), could the data we report here be equally well accounted for by the Wilson model instead of invoking the proposed FSMM? It might argued, for instance, that Wilson's non-Fourier pathway, and not the FSMM, is adapted more readily and that this accounts for our reported data. However, a number of factors argue against this explanation, such as the finding that the visual system is much less sensitive to second-order motion stimuli than to comparable first-order stimuli (Badcock & Derrington, 1985, 1989; Smith *et al.*, 1994). This would limit the extent to which adaptation in Wilson's non-Fourier pathway could be reasonably posited as an explanation of our data. Also, we have shown in a number of studies that the effects which we attribute to the FSMM are almost entirely monocular. Thus, they are unlikely to be explained by the motion units in Wilson's non-Fourier pathway because they are proposed to reside in area V2, or in area MT acting on V2 outputs, and both of these areas are highly binocular (Allman *et al.*, 1985; Bradley *et al.*, 1995; Tootell & Hamilton, 1989; Tootell *et al.*, 1983). Hence, in the present experiment, the Wilson model could not explain how the changes in plaid direction we report are confined to the exposed eye and do not exhibit IOT.

Of course, it might be that area V2 is not the crucial site for the processing of non-Fourier motion. Badcock and Derrington (1987) found that beats cannot be created dichoptically, which suggests that they are not mediated by a binocular mechanism. Together with our finding that the blob information in plaid stimuli activates a monocular mechanism, and in consequence of the fact that beats and blobs jointly define texture boundaries, they are likewise unlikely to be detected by a binocular mechanism. If this were the case, then V2 might not be the site of non-Fourier motion processing, although the claimed importance of texture boundaries in 2-D motion perception might still be justified.

Overall, we are not suggesting that the psychophysical evidence reviewed above argues conclusively against the neurophysiology claimed to underlie Wilson's non-Fourier motion processing pathway. However, it does seem to pose a significant challenge to it.

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